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Eric P. Hoberg

United States Department of Agriculture, Agricultural Research Service, geocolonizer@gmail.com

A. V. Khrustalev

K. I. Skrjabin Institute of Helminthology

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RE-EVALUATION OF *MAZAMASTRONGYLUS DAGESTANICA* (TRICHOSTRONGYLIDAE) WITH DESCRIPTIONS OF THE SYNLOPHE, GENITAL CONE, AND OTHER STRUCTURAL CHARACTERS

E. P. Hoberg and A. V. Khrustalev*

United States Department of Agriculture, Agricultural Research Service, Biosystematic Parasitology Laboratory, BARC East No. 1180, 10300 Baltimore Avenue, Beltsville, Maryland, 20705-2350

ABSTRACT: The synlophe of specimens of *Mazamastrongylus dagestanica* was characterized laterally and ventrally by a strongly tapering system of ridges in the cervical zone. This pattern, including the prominent system of “hood” ridges adjacent to the excretory pore and the absence of continuous subdorsal and subventral ridges is considered typical for the genus *Mazamastrongylus*. The synlophe of males and females was largely identical, with 37–41 ridges at the midbody. The lateral synlophe, where 2 pairs of ridges converge and terminate on the lateralmost ridge anterior to the cervical papillae appears unique for *M. dagestanica* and indicates that species-specific patterns may be recognized for *Mazamastrongylus* spp. Among male specimens, a bilobed ventral membrane, distinct from the simple and unpaired membrane, which envelops the “0” papillae, extends posterolaterally from the genital cone. It had not been described in detail previously and was also found in *M. odocoilei* and *M. pursglovei*. Characters of the bursa, genital cone, and spicules are consistent with placement of *M. dagestanica* in *Mazamastrongylus*; referral of this species to *Spiculopteragia* cannot be supported.

Specimens of the ostertagiine nematode *Mazamastrongylus dagestanica* (Altaev, 1953) were originally described as *Skrjabinagia dagestanica* Altaev, 1953 in *Ovis aries* Linnaeus from the Dagestan Republic of the Former Soviet Union. Although controversial, the present position of this species in *Mazamastrongylus* Cameron, 1935 was proposed by Jansen (1986). *Spiculopteragia alcis* Shult's, Kadenatsii, Evranova, and Schaldubin, 1954 from cervids and *Spiculopteragia popovi* Evranova, 1954 were considered to be synonyms according to Andreeva (1956) and these were later synonymized with *M. dagestanica* by Drózdź (1965) and Jansen (1958, 1986). The date for *S. alcis* is often given as 1952 (the name appears in Skrjabin et al. [1952]), however the original description apparently was published later (Skrjabin et al., 1954). Thus, by priority, *S. alcis* must be reduced as a synonym of *M. dagestanica* (see Drózdź, 1965), in contrast to the listing by Durette-Desset (1989). Although reported from sheep, the species is considered to be a typical parasite of cervids, including *Capreolus capreolus* (Linnaeus), *Alces alces* (Linnaeus), and *Cervus elaphus* Linnaeus in the Palearctic (Govorka et al., 1988; Drózdź, 1965, 1967, 1995).

The history of *M. dagestanica* is complex and has been reviewed in part by Drózdź (1965) and Hinaidy and Prosl (1981). Following the original description, this species was retained in *Skrjabinagia* (Kassimov, 1942) by Skrjabin et al. (1954). Sarwar (1957) established *Altaevia* Sarwar, 1957, referred *S. dagestanica* to the genus and distinguished it from *Spiculopteragia* (Orloff, 1933); the subfamily Spiculopteriinae was created for *Altaevia*, *Mazamastrongylus*, and *Spiculopteragia*. Jansen (1958) transferred *S. dagestanica* to *Spiculopteroides* Jansen 1958 and *S. alcis* to *Mazamastrongylus*.

Drózdź (1965) outlined the taxonomy for *S. dagestanica*, referred it to *Spiculopteragia*, and recognized *Spiculopteroides dagestanica*, *Altaevia dagestanica*, *S. alcis*, *S. popovi* Evranova, 1954, and *Mazamastrongylus alcis* as synonyms. The genus

Altaevia was reduced as a synonym of *Spiculopteragia*, but *Mazamastrongylus* was regarded as valid. The tribe Spiculopteriini (Sarwar, 1957) was established in the subfamily Ostertagiinae to contain *Spiculopteragia*, *Mazamastrongylus*, *Apteragia* Jansen, 1958, *Rinadia* Grigorian, 1951, and *Sarwaria* Drózdź, 1965.

Hinaidy and Prosl (1981) recognized the validity of *Spiculopteroides* and referred *S. dagestanica* to this genus. They also commented on the possible synonymy of this genus and *Mazamastrongylus*. Durette-Desset (1982, 1983) listed *Mazamastrongylus*, *Spiculopteroides*, *Altaevia*, and three other genera as synonyms of *Spiculopteragia*.

Jansen (1986, 1989) synonymized *Spiculopteroides* with *Mazamastrongylus* and resurrected the latter genus. Among 8 species of ostertagiines, *M. dagestanica* (with *S. alcis* as a synonym) was placed in *Mazamastrongylus*. The genus was defined by the configuration of the ventral and lateral rays of the copulatory bursa and the structure of the accessory bursal membrane (Jansen, 1986).

Durette-Desset (1989), consistent with her previous decisions, presented *Mazamastrongylus* as a synonym of *Spiculopteragia*. The species *S. dagestanica*, *S. popovi*, and *S. alcis* were referred to *Spiculopteragia* and listed independently.

Drózdź (1995) discussed polymorphism among males in several genera of ostertagiines and found this characteristic to be absent in species referred to *Mazamastrongylus*. *Mazamastrongylus dagestanica* and 4 additional species were referred to the genus.

Hoberg (1996) reevaluated the status of *Mazamastrongylus* and in agreement with Jansen (1986, 1989) and Drózdź (1995) recognized the genus as independent from *Spiculopteragia* and other genera of ostertagiines. In contrast to Jansen (1986) and Drózdź (1995), 7 species, including *M. dagestanica*, were placed in the genus (only *Sarwaria bubalis* (Sarwar, 1956) was excluded). In addition to attributes outlined by Jansen (1986), the spoon-shaped dorsal process of the spicules was considered as a defining character for *Mazamastrongylus*.

In the current study, we confirm the placement of *M. dagestanica* in the genus *Mazamastrongylus*, with reference to *Mazamastrongylus trinitatis* Cameron, 1935 (type) and other spe-

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* K. I. Skrjabin Institute of Helminthology, Central Helminthological Museum, Bol'shaya Cheryomushinskaya, 28, 117 259 Moscow, M-259, Russia.

cies. Conclusions are based on the first detailed study of the structure and configuration of the cervical synlophe and esophagus. Aspects of these characters and the bursa, genital cone, and spicules are considered within a comparative morphological context. The synlophe is compared among those species, including *Mazamastrongylus pурсglovei* (Davidson and Prestwood, 1979), *Mazamastrongylus odocoilei* (Dikmans, 1931), *Mazamastrongylus peruvianus* (Guerrero and Chávez, 1967), and *M. trinitatis*, where the pattern of longitudinal cuticular ridges has been assessed (Lichtenfels et al., 1993; Hoberg, 1996). This study represents a contribution to ongoing efforts that attempt to stabilize the generic- and species-level systematics within the Ostertagiinae (e.g., Durette-Desset, 1982, 1983, 1989; Gibbons and Khalil, 1982; Jansen, 1989; Lichtenfels and Hoberg, 1993; Hoberg and Lichtenfels, 1994; Drózd, 1995).

MATERIALS AND METHODS

Specimens were studied as temporary wholemounts cleared in phenol-alcohol (80 parts melted phenol crystals and 20 parts absolute ethanol) or in glycerine and examined with differential interference contrast light microscopy. Transverse sections of 2 males and 2 females were prepared freehand with a cataract knife and embedded in glycerine jelly. Sections were used to study the structure of the synlophe in the cervical zone (including the region of the esophageal-intestinal junction), anterior quarter, midbody, and posterior region. Figures of sections were orientated with dorsal surface toward the top of the plate and shown as if viewed from the anterior. Throughout the manuscript, measurements are presented in micrometers unless specified otherwise and presented as a range with mean \pm 1 SD in parentheses; measurements were based on 20 specimens of each sex.

The current study focused on the configuration of the synlophe, esophageal valve, and genital cone (following Lichtenfels and Pilitt, 1991; Hoberg et al., 1993a). Other meristic and structural characters are also evaluated (measurements of the ovjectors follow Lichtenfels and Pilitt [1991]). Genital papillae and bursal rays are numbered according to the methodology developed by Chabaud et al. (1970), and the terminology for the genital cone is consistent with Stringfellow (1971, 1972) and Gibbons and Khalil (1983). The orientation of the synlophe follows concepts presented by Durette-Desset (1983, 1985).

Specimens examined: *Mazamastrongylus dagestanica* (Altaev, 1953) (labeled as *Spiculopteragia alcis* Shul'ts, Kadenazii, Evranova, and Schaldubin, 1954) in *A. alces* (Linnaeus) from the Prioksko Reserve, adjacent to the Oka River approximately 160 km south of Moscow, Russia; 40 males and 40 females were examined, including 20 adult nematodes of each sex from the K. I. Skryabin Institute of Helminthology nos. 19140 and 24553.

Additional specimens for comparative purposes included: (1) U.S. National Parasite Collection (USNPC) no. 73914, *M. pурсglovei* (Davidson and Prestwood, 1979) (paratype specimens of *Apteragia pурсglovei* Davidson and Prestwood, 1979) in *Odocoileus virginianus* (Zimmermann) from South Carolina and no. 70318, *M. pурсglovei* in *O. virginianus* from Louisiana; (2) USNPC no. 29427, *M. odocoilei* (Dikmans, 1931) (type specimens of *Ostertagia odocoilei* Dikmans, 1931) in *O. virginianus* from Pennsylvania and USNPC no. 70309, *M. odocoilei* in *O. virginianus* from Georgia; (3) USNPC no. 59236, *M. peruvianus*

(Guerrero and Chávez, 1967) in alpaca (*Lama pacos* Linnaeus) from Puno, Peru; and (4) Institute of Parasitology, McGill University, Ste-Anne-de-Bellevue, Quebec, Canada, no. V000751, *M. trinitatis* Cameron, 1935 in *Mazama americana* (Erxleben) (originally listed as *Mazama simplicicornis* by Cameron [1935]) from Trinidad.

RESULTS

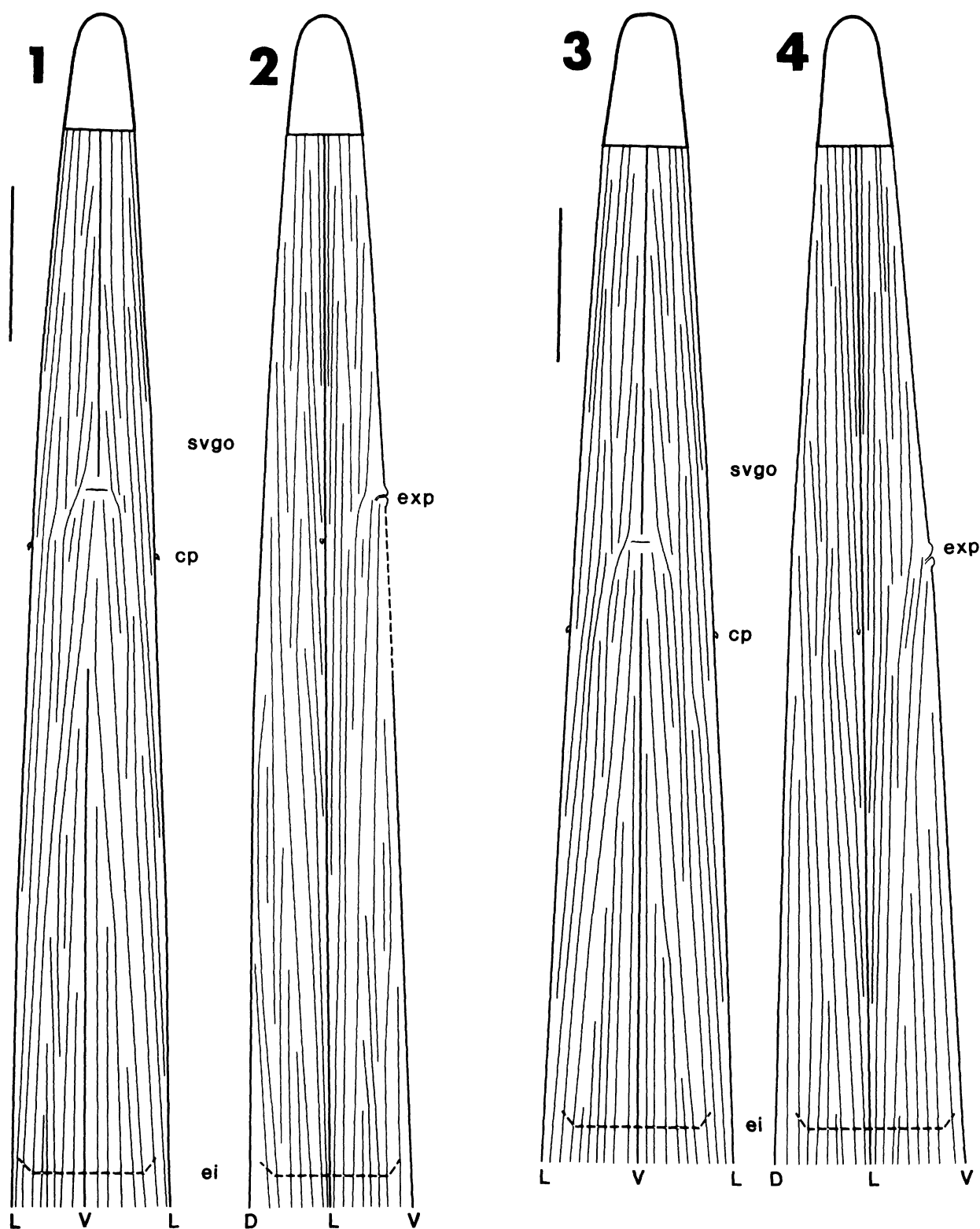
A re-evaluation of *M. dagestanica* included characters not considered in detail in the original description and subsequent redescrptions. Among these are attributes of the synlophe, esophagus, genital cone, spicules, and vulval region (Figs. 1–27). Meristic data are presented in Table I, which augment the original description, previous redescrptions, and observations presented below.

Synlophe

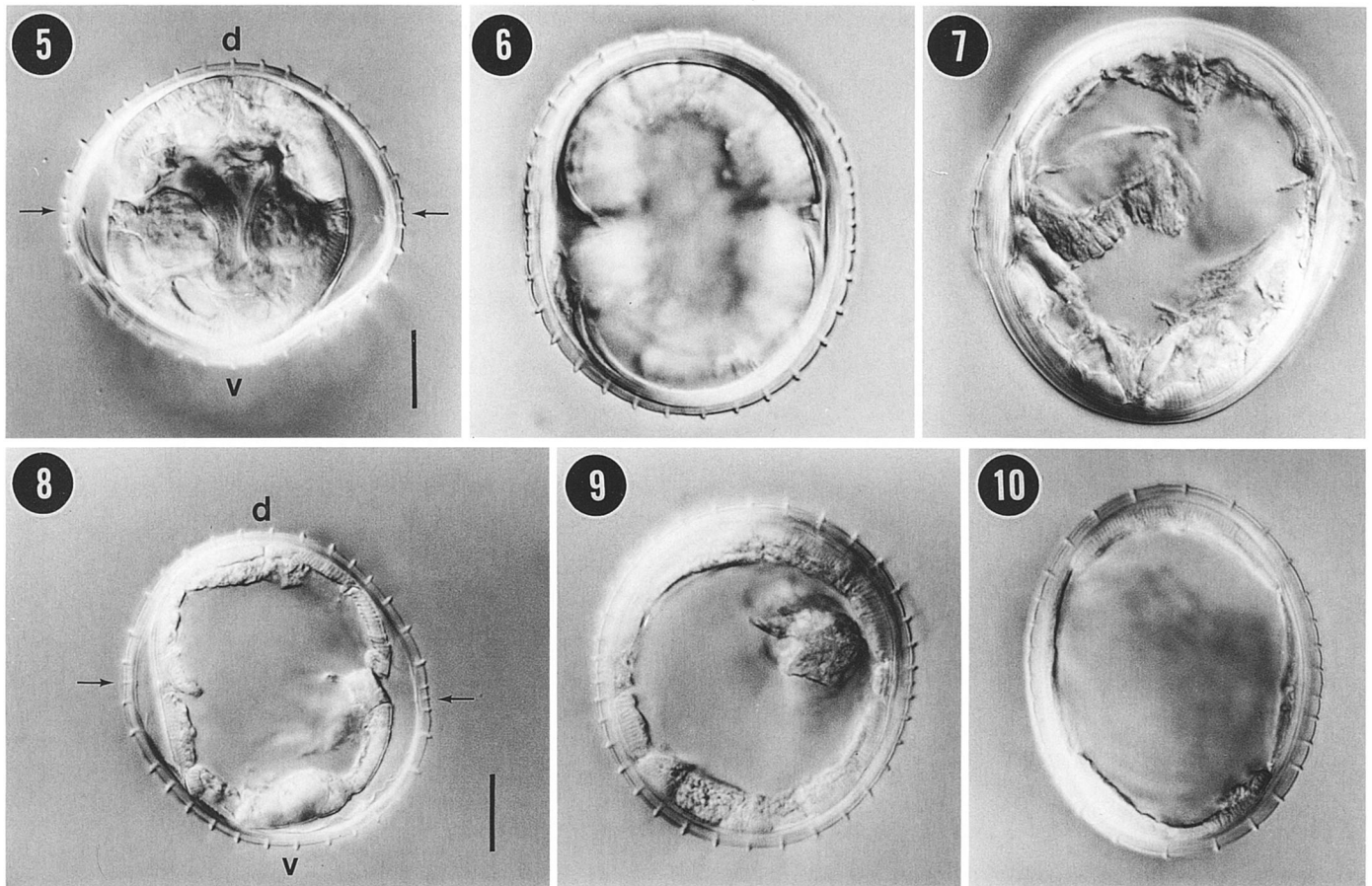
The synlophe is composed of a symmetrical system of discontinuous tapering cuticular ridges extending from the base of the cephalic expansion to near the caudal extremity in males and females (Figs. 1–4). Ridges are perpendicular to the body wall and lack a defined gradient (Figs. 5–10). In the cervical zone (anterior to the base of the esophagus), 18 ridges attain the base of the cephalic expansion. There are 29–38 ridges at the level of the minuscule thornlike cervical papillae in males. Variation in numbers is attributable to short discontinuous ridges and differences in the level of origin and termination for individual ridges in the cervical zone (Figs. 1–4). At the limit of the esophageal-intestinal (EI) junction, there are 34–36 ridges in males and 34–35 in females (Figs. 5, 8). The synlophe is of even height and the interval between ridges is less laterally than in either the dorsal or ventral fields.

Overall, the synlophe is defined by a tapering pattern in both the ventrodorsal and lateral fields. Laterally, a strongly tapering pattern is evident with 2 pairs of ridges consistently terminating anterior to the cervical papillae; posterior to the cervical papillae, variable pairs of ridges terminate adjacent to the lateralmost ridge in the cervical zone (Figs. 2, 4). Ventrally the ridges form a hood adjacent to the protruding and prominent excretory pore (Figs. 1, 3). Pairs of ridges extend posteriad across the ventral and dorsal fields to terminate on the lateralmost ridges; continuous subventral and subdorsal ridges are lacking; the synlophe is defined by 4 continuous ridges, left and right lateral and dorsal and ventral (Figs. 1–4). Variation in the ventral synlophe is evident, with 2 recognizable patterns in the cervical region posterior to the excretory pore. In 85% (n = 20 males and 20 females, respectively) of specimens the ventral ridge is discontinuous in the cervical zone, with a substantial interruption posterior to the excretory pore (Fig. 1). In 15% of specimens, a definable ventral ridge is interrupted only at the excretory pore (Fig. 3).

The tapering pattern continues for approximately 29–54% of the body from the anterior in males and 31–49% in females. In the posterior half, ridges are parallel, with 3–4 closely spaced ridges in each lateral field; in the subventral and subdorsal fields, irregular termination and origin of ridges occurs in the posterior half of the body. The synlophe extends from the cephalic extremity to near the level of the prebursal papillae in males and to the level posterior of the anus in females.



FIGURES 1-4. Synlophe in the cervical region of *Mazamastrongylus dagestanica* (Altaev, 1953) anterior to the esophageal-intestinal junction (ei) showing pattern and positions of the subventral gland orifices (svgo), excretory pore (exp), and cervical papillae (cp) in male and female specimens (scale bars = 100 μ m). 1. Ventral synlophe showing tapering pattern with ridges extending across to the lateral fields (L), typical hood ridges at level of broad liplike excretory pore, and ventral ridge interrupted posterior to the excretory pore (V); this ventral pattern is observed in 85% of male and female specimens. 2. Lateral synlophe showing strongly tapering pattern extending posterior from cervical papillae; note 2 pairs of ridges terminating anterior to the cervical papillae; dotted line indicates interrupted ventral ridge. 3. Ventral synlophe showing pattern typical of 15% of specimens in which the ventral ridge is discontinuous only at the excretory pore. 4. Lateral synlophe in specimens with alternate ventral pattern in cervical zone.



FIGURES 5–10. *Mazamastrongylus dagestanica* (Altaev, 1953) showing structure of the synlophe in transverse sections of males (Figs. 5–7) and females (Figs. 8–10) (scale bars = 20 μ m for all figures). 5. Level of esophageal–intestinal junction (EI) in male, showing 36 ridges; note minuscule lateralmost ridges (arrows) and dorsal (d) and ventral (v) ridges; ridges are perpendicular. 6. Midbody showing 37 ridges. 7. Level anterior to prebursal papillae showing retention of ridges only in lateral fields and prominent gaps in the dorsal and ventral fields. 8. Level of EI in female showing 34 ridges. 9. Midbody showing 37 ridges. 10. Posterior to the vulva, showing 32 ridges.

Posterior to the cervical zone, there are 38–42 and 41–44 ridges at the end of the first quarter in males and females; at the midbody, there are 37 and 37–41, respectively (Figs. 6, 9). A poorly defined gradient in size is evident, with ridges in the lateral fields being slightly smaller than those disposed ventrally and dorsally; the interval between ridges is also greater in the ventral and dorsal fields. In males by the third quarter there are 35–36 ridges. In the posterior, ridges terminate first ventrally at 338–637 μ m anterior to the prebursal papillae, 92–95% of body length from the anterior, and then dorsally at 234–463 μ m, 94–97% of body length from the anterior, forming arcuate gaps. Anterior to the spicules and prebursal papillae, the synlophe is lacking dorsally and ventrally and ridges decrease to 15–19 in the lateral fields, with these extending to the level of the prebursal papillae (Fig. 7).

In females, there are 35–36 ridges in the third quarter, decreasing to 32–33 posterior to the vulva (Fig. 10), with the synlophe extending to the tail.

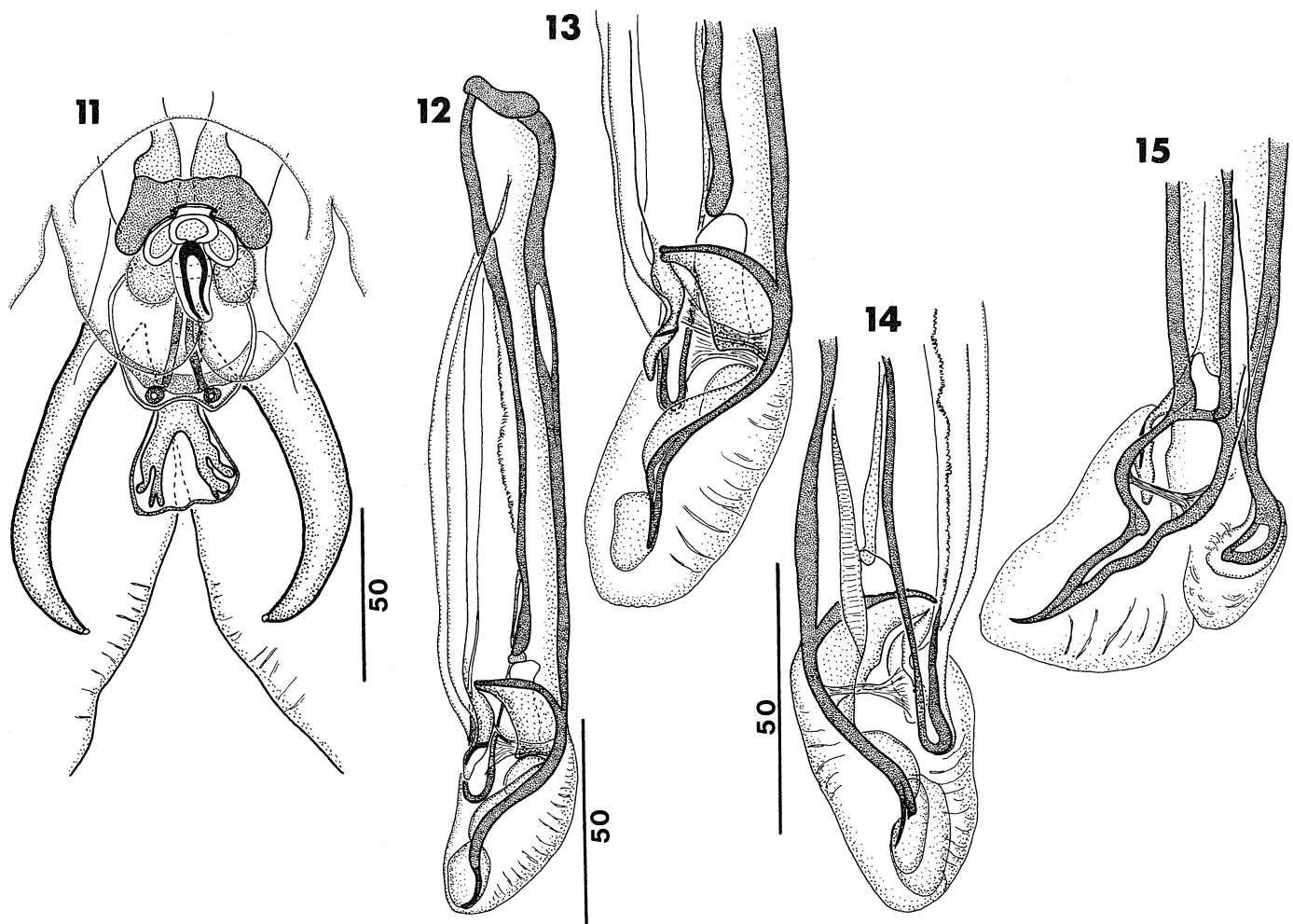
Esophagus

The esophagus is claviform, with the widest region being near the level of the esophageal–intestinal valve (EI). The orifices of

the subventral esophageal glands are located anterior to both the cervical papillae and the excretory pore (Table I). The EI valve is relatively long in males and females (81–99 μ m) (Table I; Fig. 16). A minuscule, triangular, dorsal esophageal tooth is present.

Bursal pattern and genital cone

The bursal pattern is 2-2-1 (see Durette-Desset, 1983), with rays 2 and 3 parallel throughout, and rays 4 and 5 near equal in length and divergent distally (see also Altaev, 1953; Andreeva, 1958; Drózd, 1965). The body of the genital cone is bluntly rounded (Figs. 11, 19, 21); a proconus is absent. Ventrally, a pair of lateral processes extend from the cloacal plate (Figs. 11, 20). The “0” papillae are paired, relatively long, and contained within a membrane (Figs. 11, 19, 20). A prominent bilobed membrane extending from the posterolateral margins of the ventral cloacal plate resides dorsal to the “0” papillae at the level of the ventral margin of the cloacal orifice (Figs. 11, 19, 20); proximally there are a pair of granular lobes extending into the base of the membranes (Fig. 11). The bilobed membrane is distinct and dorsal to a smaller membrane that completely en-



FIGURES 11–15. *Mazamastrongylus dagestanica* (Altaev, 1953) showing characters of the genital cone and spicules (scale bars in micrometers). 11. Genital cone in ventral view, showing “0” papillae, bilobed membrane, “7” papillae and accessory bursal membrane, and dorsal lobe. 12. Left spicule in ventral view. 13. Tip of left spicule, ventral view showing detail of structure distally. 14. Tip of left spicule in dorsal view. 15. Tip of left spicule in lateral view, from lateral to medial in orientation.

velops the “0” papillae. The accessory bursal membrane is ovoid and supported by parallel “7” papillae, which diverge distally (Figs. 11, 21). The dorsal ray is relatively short and bifurcates at approximately 60% from the anterior; distally there are 2 paired lateral processes. Rays 9/10 are contained in a dorsal lobe, positioned ventrally to ray 8 (Fig. 11).

Spicules

The spicules are complex (Figs. 12–15, 17, 18). Single dorsal and ventral processes of unequal length and degree of cuticularization originate from the respective ala at 72–80% of the spicule length from the anterior. The ventral process is sinuous and obscure, with a weakly cuticularized joint in the distal third (Figs. 12, 13, 15, 17). The dorsal process is relatively long, slender, and spoon-shaped, extending approximately half the length of the main shaft from the trifurcation (Figs. 12–15, 18). The primary shaft of each spicule is split distally and surrounded by a granular membrane (Figs. 12–14); a strutlike bar connects the cuticularized alae in an expanded region near the tip and

appears confluent with membranes associated with the dorsal and ventral processes (Figs. 13–15). The entire tip of the main shaft is encapsulated in a striated membrane (Figs. 12–15). A gubernaculum is absent.

Females

Specimens with a synlophe and esophageal structures identical to those found in males were considered to represent *M. dagestanica*. The vulva was located at 80–93% of body length from the anterior. Modification of the cuticle at the level of the vulva such as inflations were not observed. Vulval flaps were developed to varying degrees, or absent: among 40 specimens 13 had large prominent flaps (Figs. 22, 23), 14 had relatively small flaps (Figs. 24, 25) and 13 lacked a flap (Fig. 26). The lengths of the infundibula and sphincters did not differ substantially in the anterior and posterior (Figs. 24, 26; Table I). The length of the tail varied considerably (Table I); consistently several prominent annulations were present near the apex (Fig. 27).

TABLE 1. Meristic and morphological data for males and females of *Mazamastrongylus dagestanica* (Altaev, 1953) and *M. alcis* (Shul'ts, Kadenatsii, Evranova and Schaldubin, 1954) measurements in micrometers with range and mean \pm 1 SD in parentheses.

Characters	<i>M. dagestanica</i>		<i>M. dagestanica</i>		<i>M. alcis</i> †		<i>M. dagestanica</i>		<i>M. alcis</i> †	
	male	female	male	female	male	female	male	female	male	female
Body length	6,510–8,310	(7,785 \pm 547.37)	8,660	8,000–10,000	8,850–10,951	(9,992 \pm 578.02)	11,300–11,700			
Cephalic vesicle length	75–114	(95 \pm 9.01)	—	—	83–112	(100 \pm 7.32)	—			
Esophagus length	704–826	(760 \pm 29.46)	760	720–800	739–859	(777 \pm 29.14)	840–861			
Esophagus as % of body length	9.1–11.4	(9.8 \pm 0.11)	9.0	8.0–9.0	6.9–9.0	(7.8 \pm 0.50)	7.4–7.6			
Esophageal–intestinal valve length	81–99	(88 \pm 5.33)	—	—	81–99	(92 \pm 4.78)	—			
Esophageal–intestinal valve width	44–60	(53 \pm 4.30)	—	—	51–66	(57 \pm 4.93)	—			
Subventral esophageal gland orifices§	270–330	(300 \pm 16.62)	—	—	286–348	(312 \pm 13.05)	—			
Excretory pores§	281–35	(324 \pm 19.67)	340	304	304–368	(331 \pm 13.21)	287			
Cervical papillae§	338–394	(362 \pm 17.36)	410	—	337–409	(365 \pm 17.32)	410			
Spicule length	(40*) 174–208	(192 \pm 6.79)	209	244–258	—	—	—			
% Spicule anterior of trifurcation	(40*) 72–80	(73 \pm 1.74)	71	—	—	—	—			
Bursa formula	2-2-1	—	2-2-1	2-2-1	—	—	—			
Dorsal ray length	57–70	(62 \pm 3.90)	71	—	—	—	—			
Vulva position	—	—	—#	—	7,700–9,000	8,276–432.63	81			
% Body length to vulva	—	—	—	—	80–93	(83 \pm 2.58)	—			
Anterior infundibulum length	—	—	—	—	161–234	(190 \pm 16.68)	—			
Posterior infundibulum length	—	—	—	—	78–130	(106 \pm 17.16)	—			
Anterior sphincter and vestibule length	—	—	—	—	143–203	(179 \pm 14.69)	—			
Posterior sphincter and vestibule length	—	—	—	—	78–135	(99 \pm 16.00)	—			
Ovejector length	—	—	—	—	507–622	(574 \pm 30.95)	307†			
Tail length	—	—	—	—	195–265	(225 \pm 19.31)	164–276			

* Number of specimens or measurements in the present study.

§ Measured or determined from the anterior.

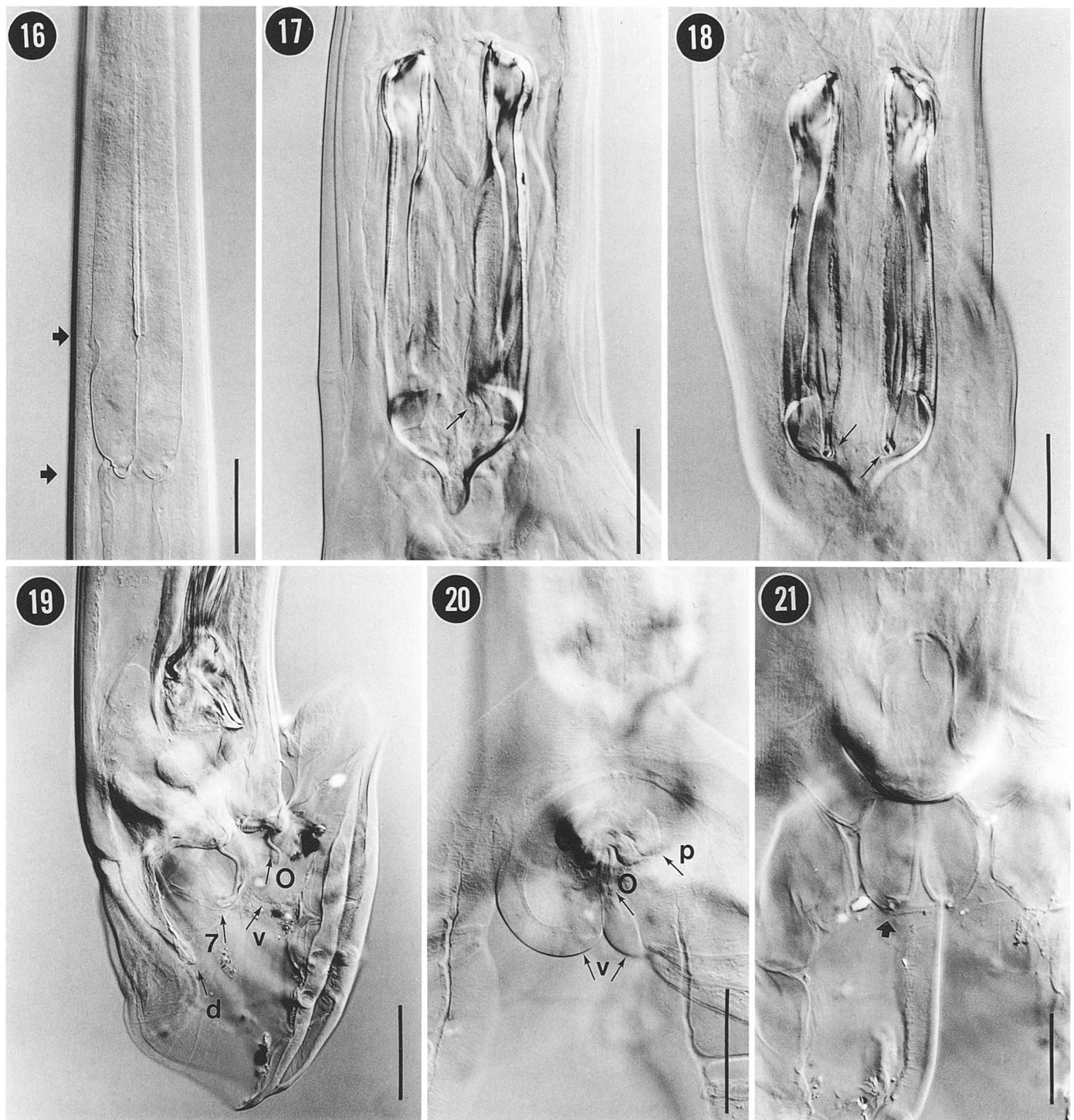
|| Estimated from published measurements.

Altaev (1953) did not give data for females.

† From Altaev (1953).

‡ From Skryabin et al. (1954).

¶ Not including infundibula.

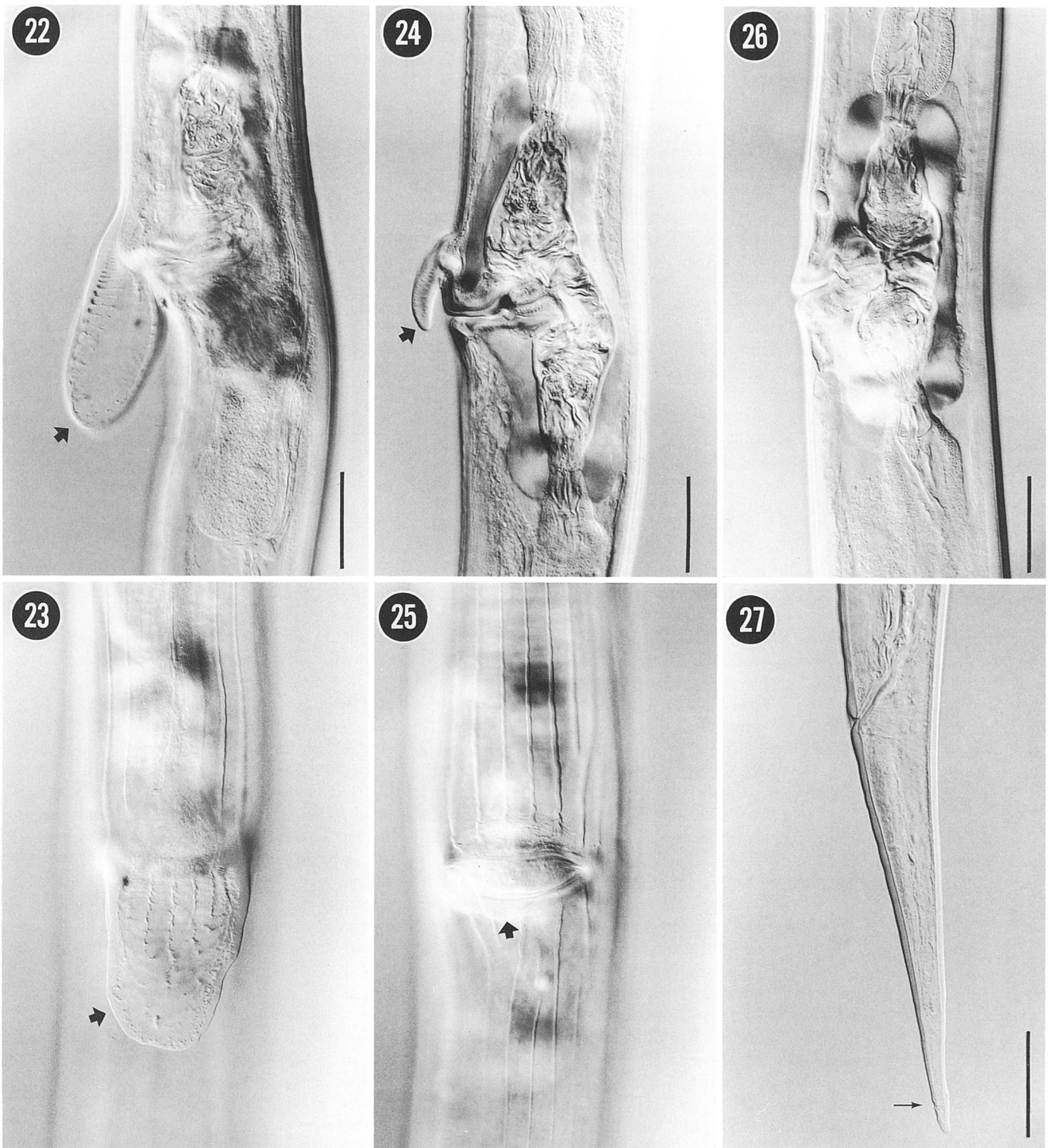


FIGURES 16–21. *Mazamastrongylus dagestanica* (Altaev, 1953) showing characters of male specimens as observed with interference contrast microscopy (scale bars = 50 μ m; Fig. 21 = 30 μ m). 16. Esophageal–intestinal valve (between arrows). 17. Spicules, ventral view showing poorly cuticularized and sinuous ventral process (arrow). 18. Spicules in dorsal view showing elongate and spoon-shaped dorsal process. 19. Bursa and genital cone in lateral view showing dorsal lobe (d), accessory bursal membrane and “7” papillae (7), bilobed ventral membrane (v), and “0” papillae (0). 20. Genital cone, ventral aspect showing lateral processes (p) extending from ventral cloacal plate, “0” papillae (0), and bilobed ventral membrane (v). 21. Genital cone, ventral view showing ovoid accessory bursal membrane and parallel “7” papillae that diverge distally.

DISCUSSION

Specimens of *M. dagestanica* as observed in the present study were generally consistent in structural and meristic characters

with original descriptions and redescrptions including those of the synonym *S. alcis* (Table I; Altaev, 1953; Skrjabin et al., 1954). The configuration of the bursa, genital cone, and spicules is consistent with placement of this species in the genus *Ma-*



FIGURES 22–27. *Mazamastrongylus dagestanica* (Altaev, 1953) showing characters of female specimens as observed with interference contrast microscopy (scales = 50 μm ; same scale for 22–25). 22, 23. Specimen with large vulval flap in lateral and ventral views (arrow). 24, 25. Specimen with small vulval flap in lateral and ventral views (arrow); note structure of ovejector (excluding the infundibula) in Figure 24. 26. Specimens lacking vulval flap shown in lateral view. 27. Tail, showing typical annulations (arrow) near apex.

zamastrongylus, based on a comparison with *M. trinitatis* (type) and other species of the genus (Jansen, 1986; Drózdź, 1995; Hoberg, 1996).

The synlophe in males and females was found to be largely identical, consisting of 34–36 continuous and short discontinuous ridges at the level of the EI junction. The numbers of ridges were found to increase posteriorly and usually attained a maximum of 38–44 in the anterior first quarter, decreasing to 37–41 at the midbody. In contrast, Altaev (1953) reported 36–38 ridges “directly in front of the genital bursa” in the original description. Specimens of *M. dagestanica* (Figs. 6, 9) had a greater number of ridges in the midbody region (37–41) as compared to all species that have been examined, except *M. peruvianus* (see Jansen, 1986; Lichtenfels et al., 1993; Hoberg, 1996).

Species of *Mazamastrongylus* in which the synlophe has been examined are all characterized by a strongly tapering pattern in the lateral and ventral fields of the cervical zone (Lichtenfels et al., 1993; Hoberg, 1996). Specimens of *M. dagestanica* share with *M. pурсglovei*, *M. odocoilei*, *M. peruvianus*, and *M. trinitatis* the prominent “hood” system adjacent to the excretory pore and absence of continuous subdorsal and subventral ridges. However, definable variation in the position and extent of the ventral ridge has not been demonstrated in these species. In *M. peruvianus*, the ventral ridge is interrupted only at the excretory pore (Hoberg, 1996). In contrast, in *M. odocoilei* and *M. pурсglovei* the ventral ridge is discontinuous in the cervical zone (Lichtenfels et al., 1993) and is similar to the predominant pattern demonstrated for specimens of *M. dagestanica*.

Laterally, the structure of the synlophe typical of *M. dagestanica* (Figs. 2, 4) appears distinct from that described for *M. odocoilei* and *M. pурсglovei* (same pattern for these species) and *M. peruvianus*. Consistently, 2 pairs of ridges converge and terminate along the lateralmost ridge anterior to the cervical papillae in specimens of *M. dagestanica*, a pattern not observed among other species. Thus, although the cervical synlophe is highly similar among those species of *Mazamastrongylus* that have been studied, species-level differences are definable. Thus, the largely identical synlophes of *M. odocoilei* and *M. pурсglovei* could indicate a common ancestor for these species of *Mazamastrongylus* and a history of cospeciation with *O. virginianus* in North America (see also comments in Lichtenfels et al. [1993]).

In females of *M. dagestanica*, vulval flaps were present in 67% of specimens examined (Figs. 22–26), but cuticular crests or irregular inflations were not observed. Specimens of *S. alcis* were described with a prominent flap at the level of the vulva (Skrjabin et al., 1954). Among other species of *Mazamastrongylus* vulval flaps may be present or absent, typical of variation in this character among ostertagiines (Lancaster and Hong, 1990). Among species of *Mazamastrongylus*, asymmetric cuticular inflations in the vulval region have been observed in specimens of *M. odocoilei*, *M. pурсglovei*, and *M. trinitatis* (see Hoberg et al., 1993b; Lichtenfels et al., 1993; Hoberg, 1996).

The structure of the bursa is of the 2-2-1 type (Altaev, 1953; Drózdź, 1965) and the configuration of the ventral and lateral rays (rays 2–5) is consistent with placement in *Mazamastrongylus* (Jansen, 1986). The genital cone and particularly the configuration of the ventral cloacal plate, accessory bursal membrane, and “7” papillae (Figs. 11, 19–21) is typical of that described for *M. trinitatis* and other species of genus (Jansen, 1986; Lichtenfels et al., 1993; Hoberg, 1996). Lateral processes bordering the ventral cloacal plate (Stringfellow, 1971) appear typ-

ical of several (Figs. 11, 20) species of *Mazamastrongylus* (see Lichtenfels et al., 1993). The “7” papillae are divergent distally and support an ovoid and weakly cuticularized accessory bursal membrane (Figs. 11, 21).

The delicate bilobed membrane on the ventral aspect of the genital cone in *M. dagestanica* has not been completely described (Figs. 11, 19, 20) and has been inconsistently depicted in published figures. For instance, the membrane was not described or shown by Altaev (1953) in the original description of *M. dagestanica*, nor was it shown in the figure of *S. alcis* provided by Drózdź (1965). However, a well developed and symmetrical bilobed membrane is shown in figures of the genital cone of *S. alcis* reproduced by Skrjabin et al. (1954) and Andreeva (1958).

The distinctly bilobed structure represents a modification of the membranes that originate on the ventral aspect of the cloaca but which reside dorsal to the ventral raylets or “0” papillae (Figs. 11, 19, 20). The ventral membrane is balloonlike in appearance and easily collapsed. It extends from the posterolateral margins of the genital cone and ventral plate, residing ventral to the cloaca and dorsal to the “0” papillae. In contrast, the “0” papillae are contained in a distinct membrane that extends from the posterior margin of the ventral plate and terminates ventral to the ventral raylets. Thus, the bilobed ventral membrane is distinct from the simple and unpaired membrane that envelops the “0” papillae as depicted by Stringfellow (1971, 1972) and Gibbons and Khalil (1983). This is further indicated, as the bilobed membrane does not extend ventrally to the “0” papillae.

The ventral membrane was consistently present in all males examined in the current study. This attribute is also present in specimens of *M. odocoilei* (seen in lateral view in Fig. 20 of Lichtenfels et al. [1993], and in type specimens, USNPC no. 29427) and in *M. pурсglovei* (based on examination of paratypes, USNPC no. 73914). In these species, the membrane is located in the same position but appears to be expanded to a lesser degree than in *M. dagestanica* (E. P. Hoberg, unpubl. obs.). This membrane was not depicted in the original description of either species from white-tailed deer (Dikmans, 1931; Davidson and Prestwood, 1979). Additionally, a characteristic bilobed membrane was depicted but not described by Drózdź (1965) in specimens of *Mazamastrongylus vietnamica* (Drózdź, 1965). Currently, this species is referred either to *Spiculopteria* by Drózdź (1995) or provisionally to *Mazamastrongylus* by Jansen (1986) and Hoberg (1996). Continued study will be necessary to reveal the potential utility of this membrane in elucidating some aspects of ostertagiine systematics.

Hoberg (1996) suggested that the structure of the spicules among species of *Mazamastrongylus* was a generic-level character. The spoon-shaped dorsal process and a sinuous and weakly cuticularized ventral process seen in *M. dagestanica* appear typical of this genus. However, the minuscule and obscure ventral process appears to be “reduced” with respect to this structure in other species. Altaev (1953) and Skrjabin et al. (1954) described a primary and dorsal process but apparently did not observe the ventral process. Additionally, the main, dorsal, and ventral processes lack trabeculate membranes, but the tip of each spicule is enveloped by a prominent striated membrane (see Hoberg, 1996). Although variation in length is apparent (Table I), structurally the spicules of *M. dagestanica* and *S. alcis* appear identical with respect to the primary and dorsal processes and terminal membranes (Altaev, 1953; Skrjabin et al., 1954).

In agreement with Jansen (1986, 1989), Drózdź (1995), and Hoberg (1996), characters of the bursa, genital cone, and spicules are consistent with placement of *M. dagestanica* in *Mazamastrongylus*. Thus, referral of this species to *Spiculoptera* as advocated by Durette-Desset (1989) cannot be supported.

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